



The littoral molluscs (Gastropoda, Bivalvia and Polyplacophora) of São Vicente, Capelas (São Miguel Island, Azores): ecology and biological associations to algae

Los moluscos litorales (Gastropoda, Bivalvia y Polyplacophora) de São Vicente, Capelas (São Miguel Island, Azores): ecología y asociaciones biológicas con algas

Sérgio P. ÁVILA*

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ABSTRACT

A two-year systematic survey was conducted in a rocky exposed shore located at Porto das Baleias (São Vicente, Capelas) in the north coast of São Miguel Island and supposedly representative of the Azorean rocky shores. Zonation of the littoral molluscs (Gastropoda, Bivalvia and Polyplacophora) was established for the most abundant species and possible molluscs/algae biological associations were studied.

Seventy-one taxa (56 Gastropoda, 13 Bivalvia and 2 Polyplacophora) were found in the 1996 and 1997 fieldwork, with a total of 35,960 specimens recorded. *Bittium* sp., an Azorean endemism, was the commonest taxon, with 11,936 and 12,374 individuals (61.1% and 75.4%, respectively in 1996 and 1997). Thirteen taxa accounted for about 96% of the total of specimens collected in both years. Some differences in the relative abundance of the commonest taxa were found between the two years. Besides *Bittium* sp., the next most abundant taxa in 1996 were *Tricolia pullus azorica* (14.0%), *Jujubinus pseudogravinae* and *Manzonina unifasciata*, both with 4%, and *Parvicardium vroomi*, *Alvania sleursi* and *Crassadoma pusio*, all between 2-3%. In 1997, *P. vroomi* and *T. pullus azorica* (6.4% and 6.1%) were the most abundant species after *Bittium* sp., followed by *Alvania sleursi* and *Jujubinus pseudogravinae* with a little more than 1% of the total number of molluscs collected in that year.

The endemic rissoids *Alvania angioyi*, *Manzonina unifasciata* and *Rissoa guernei*, the also endemic trochid *Gibbula delgadensis*, the Macaronesian *Anachis avaroides* and the small bivalve *Parvicardium vroomi* were only abundant in shallow levels (down to 5-6m), whereas the endemic rissoid *Alvania sleursi* is especially abundant below 20m depth. *Bittium* sp., *Tricolia pullus azorica* and *Jujubinus pseudogravinae* were found along all transect. No specific molluscs/algae associations were found.

RESUMEN

Se investigó durante dos años un tramo de costa rocosa expuesta en Porto das Baleias (São Vicente, Capelas) en la costa norte de São Miguel que se suponía representativa de las costas rocosas azoreanas. Se estableció la zonación de los moluscos litorales (Gastro-

* Secção de Biologia Marinha and CIRM, Departamento de Biologia, Universidade dos Açores, 9501-801 Ponta Delgada - Azores. e-mail: avila@notes.uac.pt

poda, Bivalvia y Polyplacophora) más abundantes y se estudiaron posibles asociaciones moluscos/algas.

Se encontraron 71 táxones (56 Gastropoda, 13 Bivalvia y 2 Polyplacophora) durante los años 1996 y 1997. *Bittium* sp., un endemismo azoreano, fue la especie más abundante (61,1 % y 75,4 % del total en el 96 y 97 respectivamente). Trece especies representaron el 96% del total de especímenes recolectados en ambos años. Tras *Bittium* sp, los táxones más abundantes en el 96 fueron *Tricolia pullus azorica* (14,0%), *Jujubinus pseudogravinae* y *Manzonina unifasciata*, ambos con el 4%, y *Parvicardium vroomi*, *Alvania sleursi* y *Crassadoma pusio*, entre el 2 y 3%. En el 97, tras *Bittium* sp. aparecen *P. vroomi* y *T. pullus azorica* (6,4% y 6,1%), seguidos de *Alvania sleursi* y *Jujubinus pseudogravinae* con algo más del 1%.

Los risoideos endémicos *Alvania angioyi*, *Manzonina unifasciata* y *Rissoa guernei*, el también endémico trocoideo *Gibbula delgadensis*, *Anachis avaroides* y el pequeño bivalvo *Parvicardium vroomi* solo son abundantes en los niveles someros (hasta 5-6m), mientras que *Alvania sleursi* es especialmente abundantes por debajo de 20 m. *Bittium* sp., *Tricolia pullus azorica* y *Jujubinus pseudogravinae* se encontraron a lo largo de todo el transecto. No se encontró ninguna asociación molusco/alga.

KEY WORDS: Mollusca, Azores, littoral, ecology, biological associations.

PALABRAS CLAVE: Mollusca, Azores, litoral, ecología, asociaciones biológicas.

INTRODUCTION

The first authors who studied the marine molluscs of the Azores - MAC ANDREW (1856), DROUËT (1858), MORELET (1860), DAUTZENBERG AND FISCHER (1896) and NOBRE (1924; 1930) - were mainly concerned with the publication of commented checklists. The most complete work with such a methodology is still the classic first volume of the Oceanographic Campaigns of Prince of Monaco by DAUTZENBERG (1889), where a large number of new species were described.

Since the foundation of the University of the Azores, several scientific expeditions were made by the Marine Biology team of the Department of Biology of this University to some of the islands ("Graciosa/88", "Flores/89", "Açores/89", "Santa Maria and Formigas/90", "Pico/91" and "Faial/93") providing new insights to the Azorean littoral knowledge in general and an improvement in the marine molluscs in particular (AZEVEDO AND MARTINS, 1989; GOFAS, 1989; AZEVEDO, 1990; GOFAS, 1990; AZEVEDO AND GOFAS, 1990; NETO AND AZEVEDO, 1990; AZEVEDO,

1991b; ÁVILA, 1996; ÁVILA AND AZEVEDO, 1996; ÁVILA, 1997; ÁVILA AND AZEVEDO, 1997; ÁVILA, 1998; ÁVILA, AZEVEDO, GONÇALVES, FONTES AND CARDIGOS, 1998; ÁVILA, AZEVEDO, GONÇALVES, FONTES AND CARDIGOS, 2000a; ÁVILA, GONÇALVES, FONTES AND CARDIGOS, 2000b; ÁVILA AND ALBERGARIA, 2002).

From 1996 on, a database with the littoral molluscs of the Azores (<50m) was constructed, based on samples collected in all the islands of the archipelago and an exhaustive and critical examination of literature was done. This data has provided the possibility to further understand the biogeographical relationships of the Azorean shallow-water marine molluscs (ÁVILA, 2000a).

Molluscs/algae biological associations were first studied in the Azores by CHAPMAN (1955), who was surprised by the great abundance of molluscs in a sample of *Corallina* sp. from Faial Island. Later, BULLOCK, TURNER AND FRALICK (1990) studied the micromolluscs associated to several monospecific algal fronds in the rocky intertidal. *Rissoa*

guernei Dautzenberg, 1889, *Tricolia pullus azorica* Dautzenberg, 1889, *Rissoella* sp. and *Omalogyra atomus* (Philippi, 1841) were found by these authors in high numbers associated to *Pterocliadiella capillacea*, whereas *Ulva rigida* samples had two very common small gastropods in the intertidal, *Skeneopsis planorbis* (Fabricius O., 1780) and *Omalogyra atomus*, as well as *Tricolia pullus azorica*; on *Stypocaulon scoparia* the best represented species were *Skeneopsis planorbis*, *Rissoa guernei* and *Omalogyra atomus*.

AZEVEDO (1991a) studied the malacological communities associated to the algal fronds in the littoral of São Miguel. This author found *Pisinna glabatra* (Von Mühlfeldt, 1824) and *Omalogyra atomus* to be the most abundant species in the intertidal, whereas *Omalogyra atomus* and, occasionally, *Bittium* sp. were the most abundant taxa in the infralittoral.

At Lajes do Pico (Pico Island), in a very shallow and sheltered coastal lagoon, ÁVILA (1998) found *Cingula trifasciata* (Adams J., 1798) to be the most abundant species in the intertidal, with maximum densities of 32,500 ind./m². According to BULLOCK (1995), in the intertidal of the Ilhéu de Vila Franca, an islet located in the south shores of São Miguel, *Alvania mediolittoralis* Gofas, 1989 and *Crisilla postrema* (Gofas, 1990), two rissoids, can reach densities higher than 10,000 ind./m².

More recently, COSTA AND ÁVILA (2001) have studied the molluscs associated to monospecific samples of *Halopteris filicina* and *Stypocaulon scoparia* at São Miguel Island. The samples were collected between 11 and 15m depth and these authors found that 4 taxa (*Bittium* sp., present in all of the samples and responsible for 85.6% of the total number of molluscs collected, *Setia subvaricosa* Gofas, 1989, *Tricolia pullus azorica* and *Rissoa guernei*) made up 96.6% of the total number of molluscs.

Algae provide shelter to the molluscs, protecting them against heavy waves and currents (DEAN AND CONNELL, 1987), they work as a shelter against predators (SEED, 1986; BULLOCK

ET AL., 1990) and give them food, directly through the tissues of the algae or of epiphytes diatoms or microalgae, and indirectly, through sediments and detritus that accumulate especially in the base of the algal fronds (AZEVEDO, 1991a; BULLOCK, 1995). The structural habitat complexity provided by macroalgae, usually related to higher specific richness (HICKS, 1986) is dependent upon abiotic factors such as hydrodynamic prevalent conditions, intensity and type of light and the existence of pollutants; and of biotic factors, such as predators occurrence, light competition and algal morphology, which in turn is related with the type of ramification and growth of the alga. BULLOCK ET AL. (1990) stated that algae with ramified growth, foliose or tuft-like non-coralline alga, possess a high number of micromolluscs, in contrast with species with blade-like branches (*Fucus spiralis*), filamentous algae or tuft-like coralline alga.

The main objectives of this work are to establish the zonation of the most abundant molluscs in São Miguel Island and to verify possible molluscs/algae biological associations.

MATERIALS AND METHODS

Subtidal communities off Porto das Baleias (São Vicente, Capelas) located in the north shore of São Miguel Island (Fig. 1) were surveyed under the project PRAXIS/2/2.1/BIA/169/94, "Biodiversity of the archipelago of the Azores". All samples were collected in July 1996 and July 1997 (see Table I). A transect was performed from low-tide level to 30m depth, with an extension of 450m long (Fig. 2) across a rocky bottom extensively covered by algae. *Pterocliadiella capillacea*, *Ulva* spp., *Stypocaulon scoparia*, *Asparagopsis armata*, and *Hypnea musciformis* dominated the shallow levels, whereas *Plocanium cartilagineum* and *Zonaria tournefortii* were more abundant between 10 and 30m depth. *Asparagopsis armata*, *Halopteris filicina* and *Dictyota dichotoma* were present

Table I. Samplings collected at Porto das Baleias, São Vicente, Capelas (São Miguel Island). DBUA: Reference collection of the Department of Biology of the University of the Azores.
 Tabla I. Muestras recogidas en Porto das Baleias, São Vicente, Capelas (Isla São Miguel). DBUA: Referencia en el Departamento de Biología de la Universidad de Azores.

1996			1997		
Depth (m)	Date	DBUA	Depth (m)	Date	DBUA
4	19-7-96	707/G	5	16-7-97	766
4	19-7-96	707/T	5	16-7-97	785
4	19-7-96	707/C	5	16-7-97	788
5	19-7-96	708/H	6	10/7/97	784
5	19-7-96	708/I	6	10/7/97	781
5	19-7-96	708/F	6	10/7/97	782
8	18-7-96	708/C	9	15-7-97	762
8	18-7-96	703/E	9	15-7-97	772
8	18-7-96	703/B	9	15-7-97	764
12	18-7-96	703/H	10	15-7-97	777
12	18-7-96	704/A	10	15-7-97	769+791†
12	18-7-96	704/D	10	15-7-97	771
14	17-7-96	701/B	12	14-7-97	768
14	17-7-96	701/A	12	14-7-97	778
14	17-7-96	701/C	12	14-7-97	776
16	17-7-96	702/D	15	11/7/97	783
16	17-7-96	702/E	15	11/7/97	779
16	17-7-96	702/H	15	11/7/97	787
22	16-7-96	694/D	20	11/7/97	780+790
22	16-7-96	692/B	20	11/7/97	767
22	16-7-96	693/C	20	11/7/97	786
27	15-7-96	690/B	25	12/7/97	763+773
27	15-7-96	691/C	25	12/7/97	774
27	15-7-96	689/A	25	12/7/97	789
			30	14-7-97	770
			30	14-7-97	775
			30	14-7-97	765

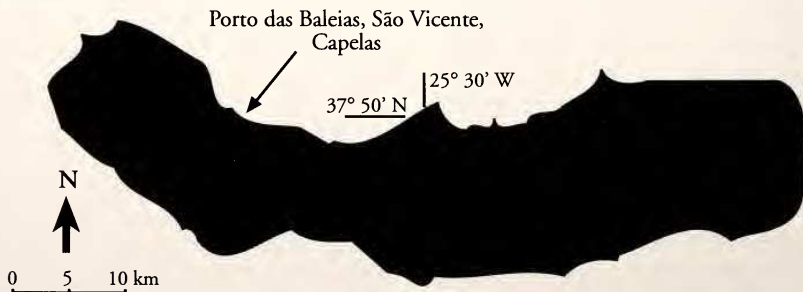


Figure 1. São Miguel Island (Azores), with the location of Porto das Baleias, São Vicente, Capelas.
 Figura 1. Isla São Miguel (Azores), con la localización de Porto das Baleias, São Vicente, Capelas.

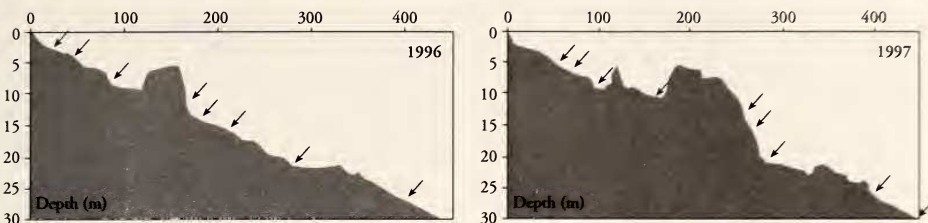


Figure 2. Profile of the transects, Porto das Baleias, São Vicente, Capelas (São Miguel, Azores) in 1996 and 1997. The arrows show the sampling sites of the 3 replicates.

Figura 2. Perfil de los transectos, Porto das Baleias, São Vicente, Capelas (São Miguel, Azores) en 1996 y 1997. Las flechas muestran los lugares de muestra de las 3 réplicas.

along all transect. In most of the transect, large boulders were dominant, but especially bellow 20m depth, there were large areas of bedrock interspersed with sandy patches.

Minimum area for quantitative studies of algae in the Azorean sublittoral is 50x50cm (NETO, 1997) larger than the minimum area determined for molluscs (25x25cm) (AZEVEDO, 1991a) so the former area was used. Three

quadrates were scrapped in each selected depth; the algae collected were put in a labeled cotton drawstring bag. In the laboratory, samples were washed several times with seawater and animals were removed by pouring the washing water through 1 mm, 0.5 mm and 0.25 mm mesh sieves. Samples were labeled and preserved in 70% ethanol. After draining for about 30min, the wet weight of the algae was determined

Table II. Most common taxa/species found at Porto das Baleias, São Vicente, Capelas during the 1996 and 1997 campaigns. n: total number of specimens collected.

Tabla II. Especies más comunes en Porto das Baleias, São Vicente, Capelas durante las campañas de 1996 y 1997. n: número total de especímenes recolectados.

	1996	1997	1996	1997
	n	n	%	%
<i>Bittium</i> sp.	11,936	12,374	61.1	75.4
<i>Tricolia pullus azorica</i>	2,737	993	14.0	6.1
<i>Parvicardium vroomi</i>	557	1042	2.9	6.4
<i>Jujubinus pseudogravinae</i>	753	216	3.9	1.3
<i>Manzonina unifasciata</i>	719	78	3.7	0.5
<i>Alvania sleursi</i>	526	284	2.7	1.7
<i>Crassadoma pusio</i>	442	36	2.3	0.2
<i>Cardita calyculata</i>	320	117	1.6	0.7
<i>Alvania angioyi</i>	205	159	1.1	1.0
<i>Ocenebrina aciculata</i>	145	162	0.7	1.0
<i>Anachis avaroides</i>	168	108	0.9	0.7
<i>Gibbula delgadensis</i>	62	160	0.3	1.0
<i>Rissoa guernei</i>	155	35	0.8	0.2
Total	18,725	15,764	96.0	96.2
TOTAL (all taxa)	19,540	16,420	100.0	100.0

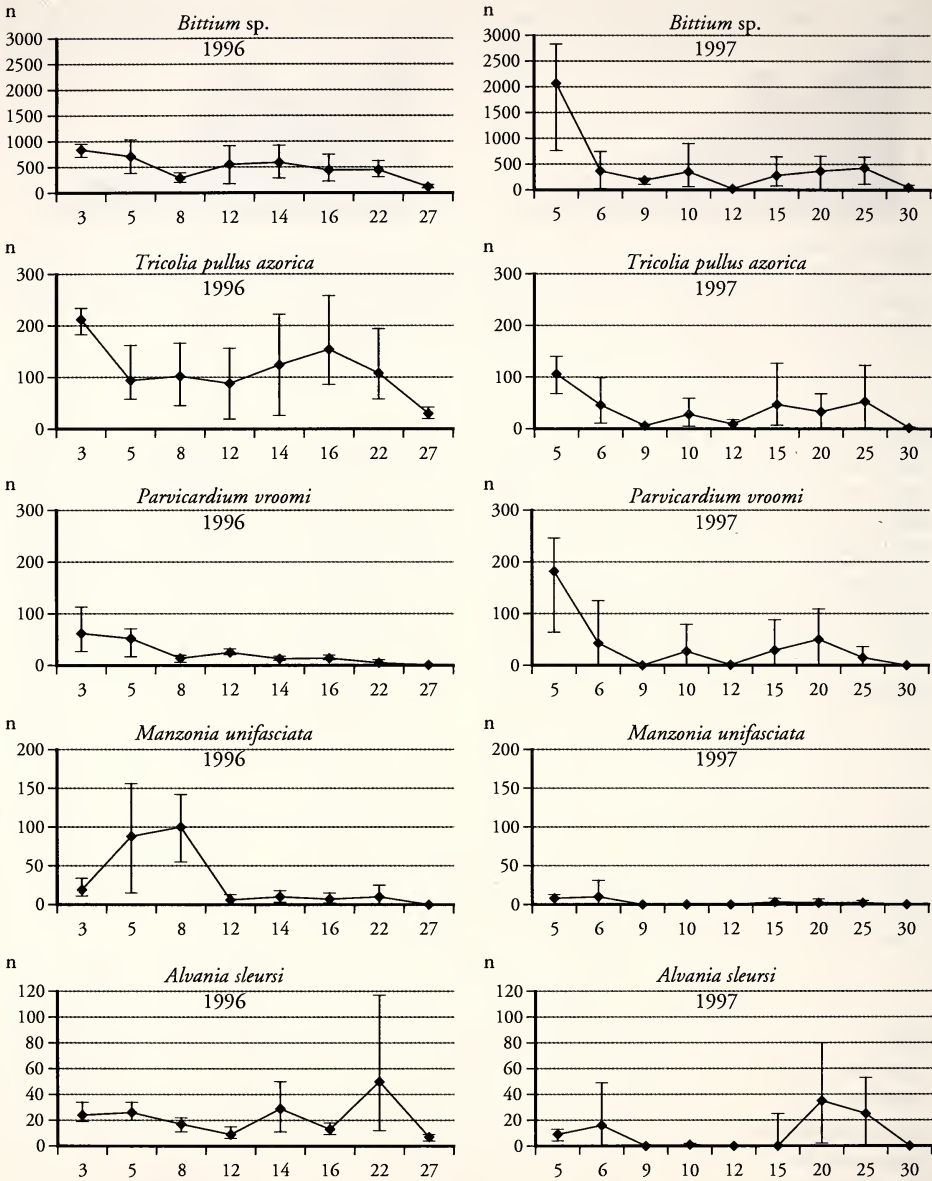


Figure 3. Zonation of the most common molluscs species in 1996 and 1997 at Porto das Baleias, São Vicente, Capelas (São Miguel, Azores) (maximum, mean and lower values by depth).
 Figura 3. Zonación de las especies de moluscos más comunes en 1996 y 1997 en Porto das Baleias, São Vicente, Capelas (São Miguel, Azores) (valores máximo, medio y mínimo por profundidad).

($\pm 0,01g$). All molluscs found in the 1 mm mesh sieve were sorted, identified and counted (see Appendices 1 and 2). Only live molluscs were counted. Mol-

luscs retained in the 0.5 mm and 0.25 mm mesh sieves will be studied in future works. About 300 days were spent just sorting the material. All

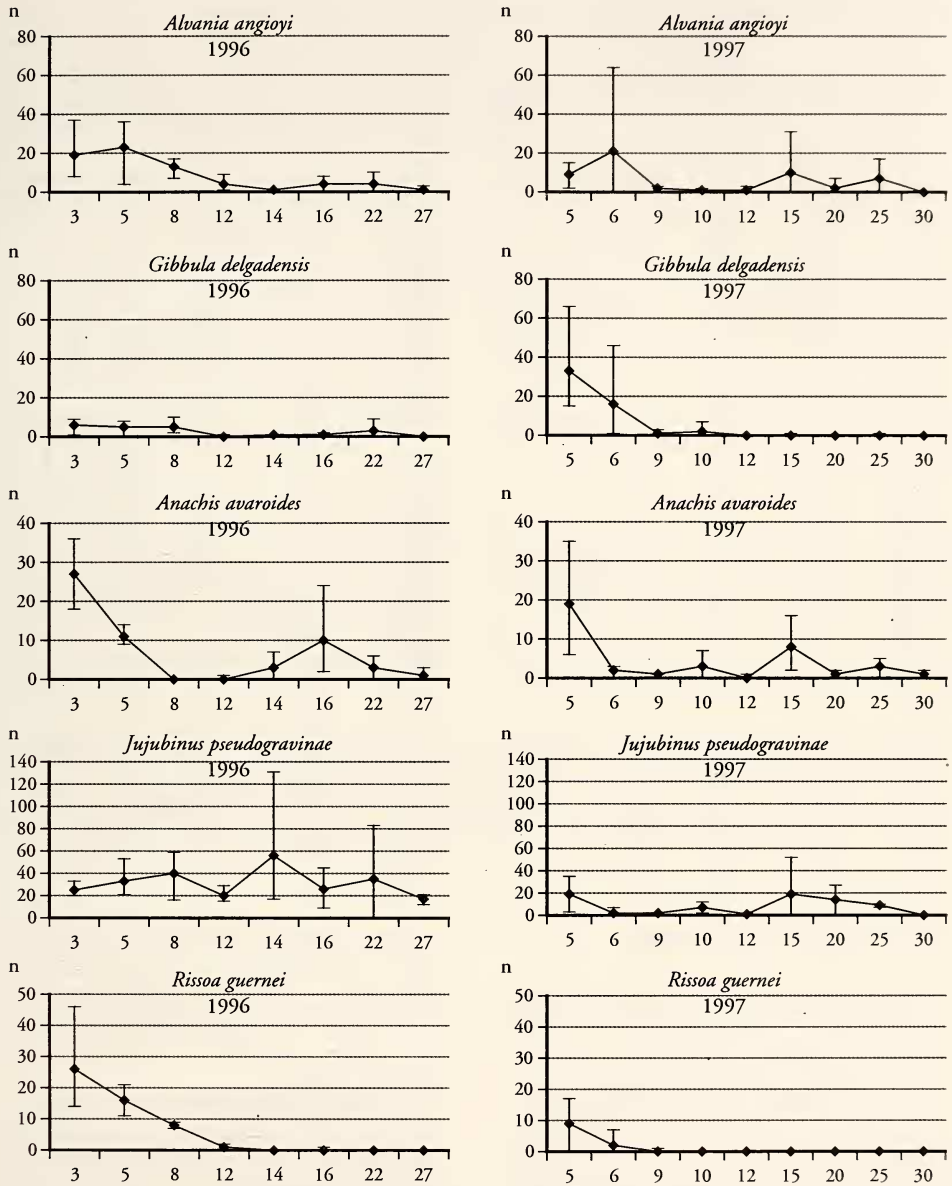


Figure 3. Continuation.
 Figura 3. Continuação.

samples were given a number and were deposited in the DBUA (Department of Biology of the University of the Azores) marine molluscs reference collection.

Most problematic molluscan taxa were photographed under the scanning

electronic microscope (protoconch, teleoconch, and microsculpture of both); these photos were quite useful in the posterior identification. Algae were identified by Dra. Ana Neto (University of the Azores).

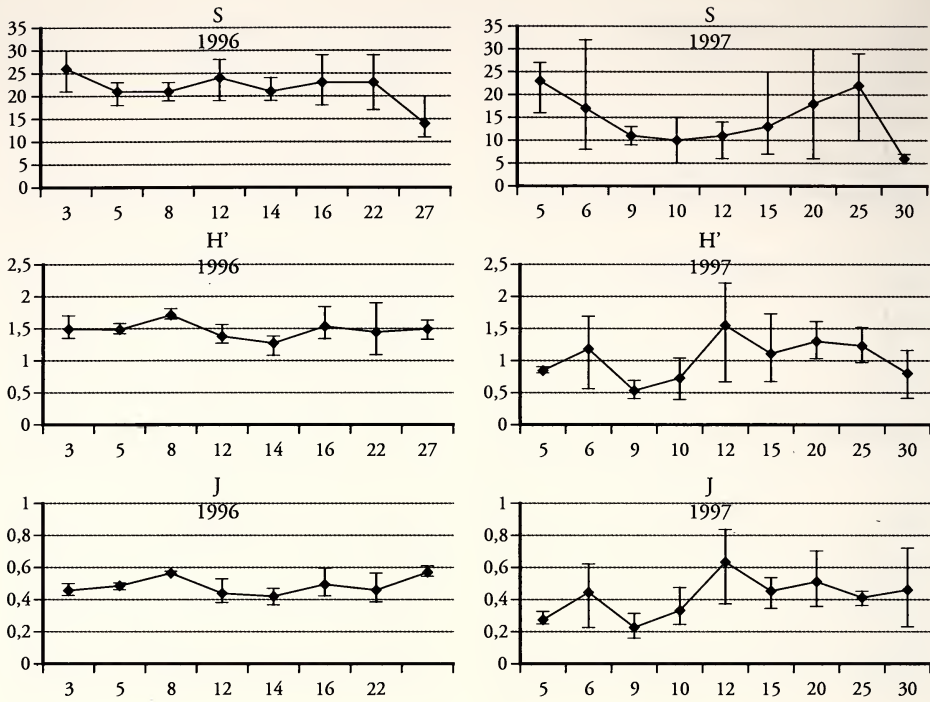


Figure 4. Taxa/species number (S), diversity index of Shannon-Wiener (H') and equitability index (J) by depth in 1996 and 1997 (maximum, mean and lower values by depth).
 Figura 4. Número de especies (S), índice de diversidad de Shannon-Wiener (H') e índice de equitabilidad (J) por profundidades en 1996 y 1997 (valores máximo, medio y mínimo por profundidad).

STATISTICAL ANALYSIS

Data were analyzed with the statistical package PRIMER (version 5.2) (Plymouth Routines in Multivariate Ecological Research - Plymouth Marine Laboratory). For each depth sampled in both campaigns (1996 and 1997), zonation graphs were constructed for the most abundant taxa with maximum, mean and lower density values.

Species diversity was calculated in each quadrat, using species richness (S) and diversity indices of Shannon-Wiener (H') and evenness (J) (KREBS, 1989; BEGON, HARPER AND TOWNSEND, 1996).

Multivariate analysis was performed, with raw data transformed by \sqrt{x} (FIELD, CLARKE AND WARWICK, 1982; CLARKE AND AINSWORTH, 1993). In Q-analysis, dendrograms were con-

structed with Bray-Curtis similarity index followed by UPGMA method (FIELD ET AL., 1982); R-analysis was also performed, dendrograms constructed by using Euclidean distance and UPGMA method.

ANOSIM/PRIMER program ("randomization/permutation test") (WARWICK AND CLARKE, 1993) was used with 20,000 permutations, to test differences between pre-selected groups of samples. This program results in a value of R, between -1 and +1 (usually, $R > 0$). If $R = 1$, this means that all replicates of a given depth are more similar than any replicates of different depths; if $R \approx 0$, the similarity between replicates is independent of its depth and will be similar, in average (CLARKE AND WARWICK, 1994).

Species with a ratio > 1.40 (SIMPER/PRIMER analysis) were considered as

Table III. Diversity indices by quadrat in 1996 and 1997. S: number of taxa/species; H': diversity index of Shannon-Wiener; J: index of equitability.

Tabla III. Índices de diversidad por cuadrado en 1996 y 1997. S: número de especies; H': índice de diversidad de Shannon-Wiener; J: índice de equitabilidad.

1996					1997				
Quadrat	Depth	S	H'	J	Quadrat	Depth	S	H'	J
1	3	28	1.42	0.426	1	5	16	0.90	0.326
2	3	21	1.35	0.443	2	5	27	0.82	0.248
3	3	30	1.70	0.500	3	5	26	0.81	0.248
4	5	23	1.58	0.504	4	6	32	1.69	0.486
5	5	23	1.45	0.462	5	6	12	0.56	0.226
6	5	18	1.42	0.491	6	6	8	1.29	0.622
7	8	20	1.67	0.556	7	9	9	0.69	0.314
8	8	23	1.81	0.577	8	9	11	0.50	0.207
9	8	19	1.65	0.560	9	9	13	0.41	0.159
10	12	19	1.56	0.529	10	10	15	0.75	0.276
11	12	25	1.30	0.405	11	10	5	0.39	0.245
12	12	28	1.27	0.3861	12	10	9	1.04	0.475
13	14	24	1.35	0.424	13	12	14	2.21	0.837
14	14	19	1.38	0.470	14	12	6	0.67	0.373
15	14	19	1.08	0.367	15	12	13	1.77	0.691
16	16	29	1.42	0.423	16	15	7	0.67	0.345
17	16	18	1.34	0.465	17	15	7	0.93	0.476
18	16	22	1.84	0.595	18	15	25	1.73	0.537
19	22	23	1.34	0.427	19	20	18	1.03	0.357
20	22	17	1.09	0.385	20	20	30	1.61	0.473
21	22	29	1.90	0.565	21	20	6	1.26	0.703
22	27	11	1.33	0.555	22	25	27	1.20	0.363
23	27	12	1.52	0.610	23	25	10	0.97	0.422
24	27	20	1.63	0.545	24	25	29	1.52	0.452
					25	30	7	0.83	0.429
					26	30	5	1.16	0.721
					27	30	6	0.41	0.231

mainly responsible for the differences detected between pre-selected groups (WARWICK, PLATT, CLARKE, AGARD AND GOBIN, 1990). Three groups were selected, based on the empirical knowledge of the transect's bottom characteristics: shallow levels (until 10m depth), medium depths (between 10 and 20m depth) and deeper levels (from 20 down to 30m depth). These pre-selected groups were designed by the letters s ("shallow"), m ("medium") and d ("deep"), respectively.

DAFOR scale, [D-dominant (>75%); A-abundant (50%); F-frequent (25%); O-occasional (10%); R-rare (5%)] was used

to measure the relative abundance of the algae species. As this is a semi-quantitative scale, in contrast to the quantitative molluscs data, the latter were transformed accordingly, in order to test possible molluscs/algae biological associations. A multivariate analysis was conducted over the semi-quantitative molluscs-algae data (most abundant species in both 1996 and 1997) and dendrograms were constructed using Bray-Curtis similarity index followed by UPGMA. Euclidean distance was used to construct the dendrograms of the analysis of pooled semi-quantitative molluscs-algae data.

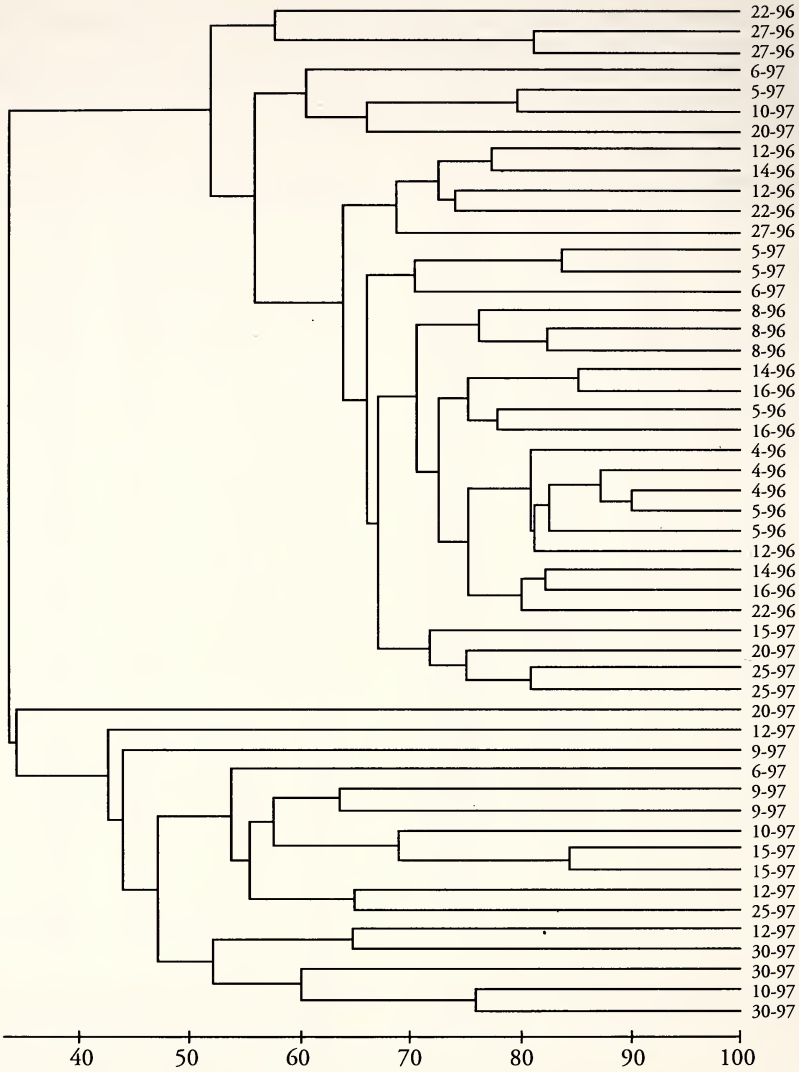


Figure 5. All replicates of 1996 and 1997 grouped by depth-year. Data transformed by $\sqrt{\sqrt{x}}$, Bray-Curtis similarity index, UPGMA.

Figura 5. Total de réplicas de 1996 y 1997 agrupadas por profundidad-año. Datos transformados por $\sqrt{\sqrt{x}}$, índice de similaridad de Bray-Curtis, UPGMA.

RESULTS

A total of 35,960 specimens were counted in both 1996 and 1997 campaigns at São Vicente, Capelas, belonging to 71 taxa (56 Gastropoda, 13 Bivalvia and 2 Polyplacophora). Of those, 19,540 specimens were collected in

1996 and 16,420 in 1997. Forty-one taxa were found in both years (see Appendices 1 and 2), 11 and 17 taxa exclusively in 1996 and 1997, respectively.

Bittium sp. was the commonest taxa, with 11,936 and 12,374 individuals (61.1% and 75.4%, respectively in 1996 and 1997). Thirteen taxa accounted for

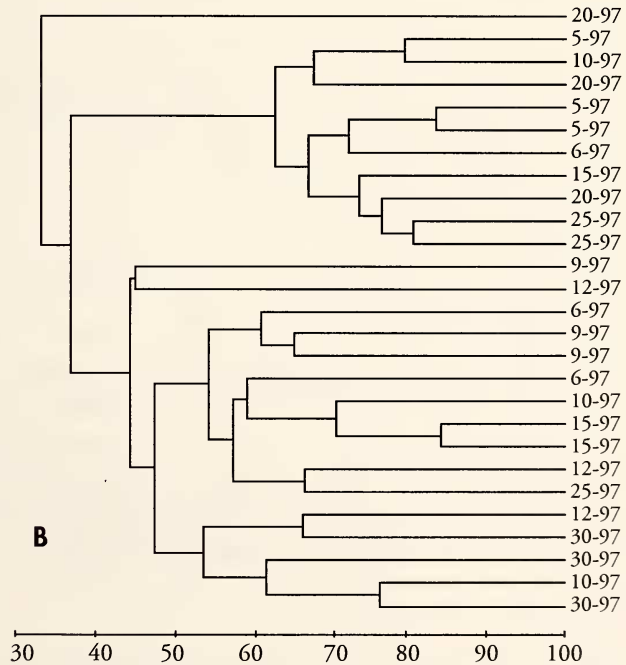
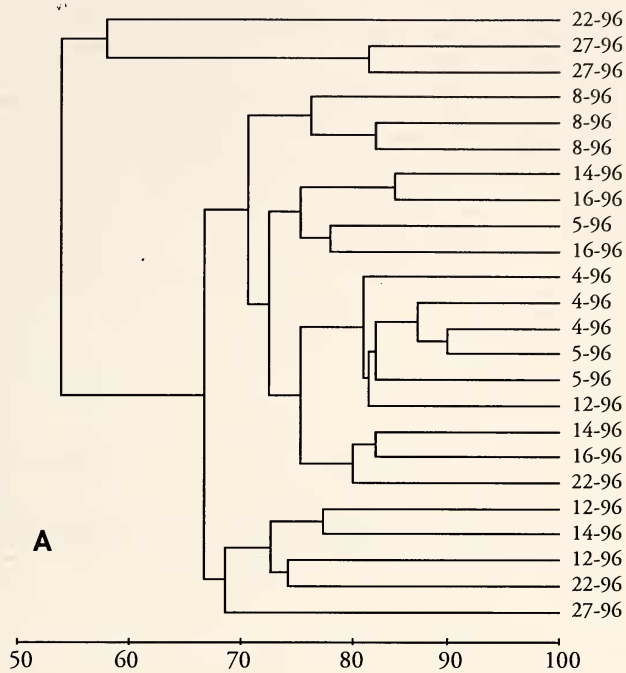


Figure 6. A: replicates of 1996; B: replicates of 1997 (grouped by depth-year). Data transformed by $\sqrt{\sqrt{x}}$, Bray-Curtis similarity index, UPGMA.

Figura 6. A: réplicas de 1996; B: réplicas de 1997 (agrupadas por profundidad-año). Datos transformados por $\sqrt{\sqrt{x}}$, índice de similitud de Bray-Curtis, UPGMA.

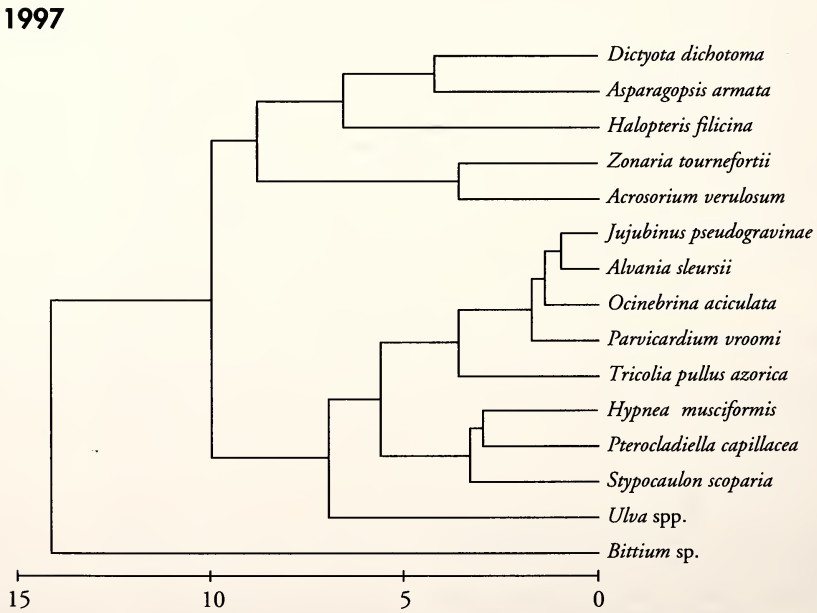
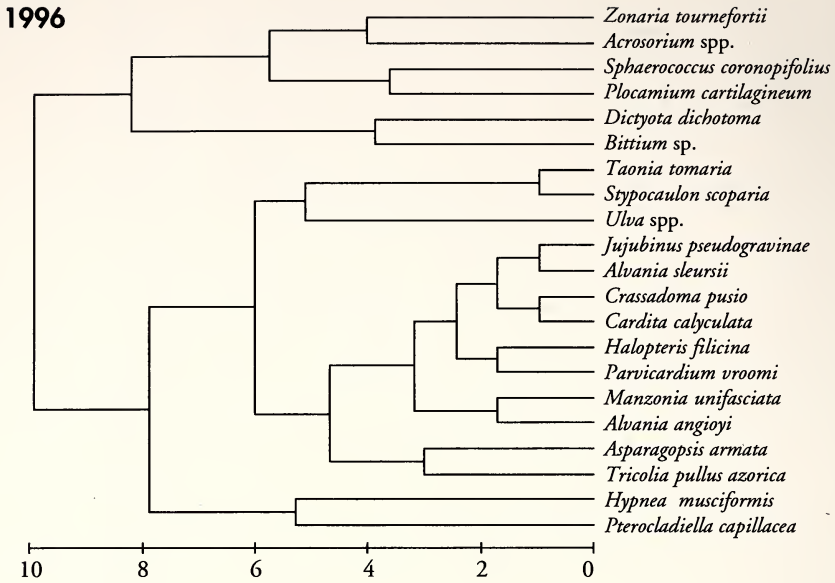


Figure 7. Mollusc/algae collected in 1996 and 1997. Non-transformed semi-quantitative data, DAFOR scale. Euclidean distance, UPGMA.

Figura 7. Moluscos/algas recolectados en 1996 y 1997. Datos semicuantitativos no transformados, escala DAFOR. Distancias euclidianas, UPGMA.

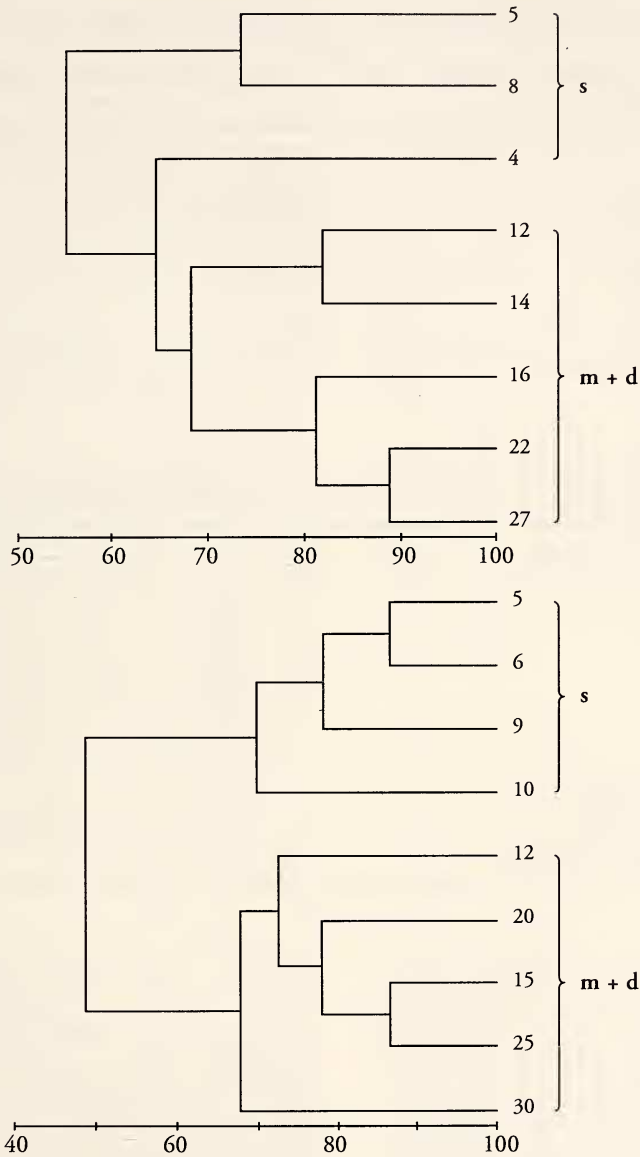


Figure 8. Molluscs/algae collected in 1996 and 1997. Non-transformed semi-quantitative data, DAFOR scale. Bray-Curtis similarity index, UPGMA.

Figura 8. Moluscos/algas recolectados en 1996 y 1997. Datos semicuantitativos no transformados, escala DAFOR. Índice de similitud de Bray-Curtis, UPGMA.

about 96% of the total of specimens collected in both campaigns (see Table II). Some differences in the relative abundance of the commonest taxa were

found between the two years. Besides *Bittium* sp., most abundant taxa in 1996 were *Tricolia pullus azorica* (14,0%), *Jujubinus pseudogravinae* Nordsieck, 1973

Table IV. Pre-defined groups and symbols used in the multivariate analysis with ANOSIM and SIMPER programs.

Tabla IV. Grupos predefinidos y símbolos usados en el análisis multivariantes con los programas ANOSIM y SIMPER.

Pre-defined groups	Depth (m) - year
s96 – shallow water, 1996	4-96; 5-96; 8-96
s97 – shallow water, 1997	5-97; 6-97; 9-97; 10-97
m96 – medium water, 1996	12-96; 14-96; 16-96
m97 – medium water, 1997	12-97; 15-97; 20-97
d96 – deep water, 1996	22-96; 27-96
d97 – deep water, 1997	25-97; 30-97

Table V. ANOSIM results. Data transformed by $\sqrt{\sqrt{x}}$. Other symbols as in Table IV.

Tabla V. Resultados de ANOSIM. Datos transformados por $\sqrt{\sqrt{x}}$. Resto de símbolos como en la Tabla IV.

Comparisons between groups	R
s96 / s97	0.277
m96 / m97	0.430
d96 / d97	0.431
s97 / m97	0.039
m97 / d97	-0.031
d96 / m97	0.137
(s96-s97) / (m96-m97)	0.056
(s96-s97) / (d96-d97)	0.198
(m96-m97) / (d96-d97)	0.046
(s96-m96-d96) / (s97-m97-d97)	0.337

and *Manzonina unifasciata* (Dautzenberg, 1889), both with 4%, and *Parvicardium vroomi* van Aartsen, Menkhorst and Gittenberger, 1984, *Alvania sleursi* (Amati, 1987) and *Crassadoma pusio* (Linnaeus, 1758), all between 2-3%. In 1997, *P. vroomi* and *T. pullus azorica* (6,4% and 6,1%) were the most abundant species after *Bittium* sp., followed by *Alvania sleursi* and *Jujubinus pseudogravinae* with a little more than 1% of the total number of molluscs collected in that year. *Bittium* sp. was found in all quadrates sampled in 1996 and 1997, whereas *A. sleursi*, *C. pusio* and *T. pullus azorica* were present in all quadrates in 1996 (Appendices 1 and 2).

Some species were clearly only abundant in shallow levels (down to 5-6m) as the endemic rissoids *Alvania*

angioyi van Aartsen, 1982, *Manzonina unifasciata* and *Rissoa guernei*, the also endemic trochid *Gibbula delgadensis* Nordsieck, 1982, the Macaronesian *Anachis avaroides* Nordsieck, 1975 and the small bivalve *Parvicardium vroomi*. On the other side, the endemic rissoid *Alvania sleursi*, is especially abundant below 20m depth, whereas *Bittium* sp., *Tricolia pullus azorica* and *Jujubinus pseudogravinae* were found along all transect. The highest variation detected when both years are compared, is related to the higher abundance of *Bittium* sp. at 5m in 1997 (Fig. 3).

Species number and diversity indices of Shannon-Wiener (H') and evenness (J), show lower variations between replicates by depth in 1996 when compared to 1997 (cf. Table III and Fig. 4).

When all 1996 and 1997 replicates are pooled, the dendrogram (Q-analysis) shows a clear split of replicates by year (Fig. 5). Besides, and with only a few exceptions, most of the clusters are among replicates of similar depths. A similar analysis by year shows that in 1996, replicates follow the depth gradient (Fig. 6A); in contrast, 1997 replicates do not show such an evident pattern, with higher mixture of replicates of different depths/levels (cf. Fig. 6B).

Cluster analysis of pooled algae-molluscs data (Euclidean distance) is not particularly elucidative. In the 1996 campaign (Fig. 7), *Bittium* sp. clusters with the alga *Dictyota dichotoma*, *Parvicardium vroomi* clusters with *Halopteris filicina* and *Tricolia pullus azorica* clusters with *Asparagopsis armata*. In the 1997 campaign, a strong dichotomy between molluscs and algae was found, no molluscs being associated to any alga species. If the same procedure (cluster analysis of pooled algae-molluscs data) is repeated, now in R-mode, there is a clear separation between shallow levels (s) and medium-deep depths (Fig. 8).

Major differences among pre-defined groups (see Table IV) do occur between medium depth replicates of 1996 and 1997 (m96/m97), between the deepest levels of 1996 and 1997 (d96/d97) and between all samples of 1996 and 1997 (s96-m96-d96 / s97-m97-d97) (see Table V).

Average similarity values of pre-defined groups (s, m, d) is higher in 1996 than in 1997, *Bittium* sp. and *Tricolia pullus azorica* being responsible for this. Average similarity decreases with depth, when the same level is compared in the two years (s96/s97, m96/m97 and d96/d97). Similarities among shallow and medium depth levels are best explained by the two previous taxa plus *Jujubinus pseudogravinae*. In the deepest levels (d96/d97), we must add the muricid *Ocinebrina aciculata* (Lamarck, 1822) to *Bittium* sp. and *Tricolia pullus azorica* (cf. Table VI).

Crassadoma pusio and *Alvania sleursi* are responsible for most of the differ-

ences detected between levels (s96/s97, m96/m97 e d96/d97), their importance increasing with depth. Actually, total number of *Crassadoma pusio* individuals in 1997 is less than 10% the number in 1996; *Alvania sleursi* specimens in 1997 are about half total numbers in 1996. In 1996, *Rissoa guernei* and *Alvania angioyi*, both common species in the shallow levels, distinguish these levels from the medium and deep ones, *Parvicardium vroomi*, uncommon from 20m on, explaining the medium-deep level differences together with *Bittium* sp. In 1997, *Bittium* sp. and *Tricolia pullus azorica* splits medium from deep levels. When all levels are pooled by year (s96-m96-d96 / s97-m97-d97), *Alvania cancellata*, *Alvania sleursi*, *Crassadoma pusio* and *Manzonina unifasciata* (more abundant in 1996), and *Bittium* sp. and *Parvicardium vroomi* (more abundant in 1997) are responsible for the differences detected (Table VII).

DISCUSSION

No specific molluscs/algae associations were found in this work, however, a certain algal preference was detected because of the high densities of a few molluscan taxa in some algae. The most obvious examples were *Bittium* sp. in *Halopteris filicina* and *Pterocliadiella capillacea*, *Parvicardium vroomi* in *Halopteris filicina*, and *Tricolia pullus azorica* in *Asparagopsis armata*, *P. capillacea* and *Dictyota dichotoma*. It appears that the algae provide a good microhabitat for the molluscs, rather than being their main source of food. It is interesting to note the common presence of *Tricolia pullus azorica* in *Asparagopsis armata*, a red algae that is usually devoid of molluscs. This algae was introduced into the Atlantic and Mediterranean in the beginning of the 20th century (FELDMANN AND FELDMANN, 1942) and is now widely distributed in the north-eastern Atlantic, from the British isles south to Senegal, the Azores, Madeira and Canary Islands (DIXON, 1964).

Table VI. SIMPER results. Data transformed by $\sqrt{\sqrt{x}}$. Aan: *Alvania angioyi*; Aca: *Alvania cancellata*; Asl: *Alvania sleursi*; Ana: *Anachis avaroides*; Bit: *Bittium* sp.; Car: *Cardita calyculata*; Cra: *Crassadoma pusio*; Gib: *Gibbula delgadensis*; Juj: *Jujubinus pseudogravinae*; Man: *Manzonina unifasciata*; Mar: *Marshallora adversa*; Nas: *Nassarius incrassatus*; Oci: *Ocinebrina aciculata*; Par: *Parvicardium vroomi*; Ris: *Rissoa guernei*; Tri: *Trichomusculus semigranatus*; Tpa: *Tricolia pullus azorica*. Other symbols as in Table IV.

Groups	Average similarity	Taxa/Species
s96	76.29	Bit - Tpa - Man - Juj - Par - Asl - Ris - Aan
m96	72.58	Bit - Tpa - Juj - Par - Cra - Asl - Car
d96	45.71	Bit - Tpa - Asl - Cra - Oci
s97	47.33	Bit - Tpa
m97	42.28	Bit
d97	45.71	Bit - Tpa - Mar
s96 / s97	53.10	Bit - Tpa - Juj - Nas
m96 / m97	50.10	Bit - Tpa - Juj - Nas
d96 / d97	45.83	Bit - Tpa - Oci
(s96-m96-d96)	67.13	Bit - Tpa - Juj - Asl - Cra - Par - Car - Man - Oci - Aca - Nas
(s97-m97-d97)	43.88	Bit - Tpa

BULLOCK ET AL. (1990) did not find also any specific biological associations of molluscs to algae in São Miguel Island. According to these authors, the majority of the molluscs found in their samples were common in several species of algae (e.g.: *Omalogyra atomus*, very common in *Pterocladia capillacea* and *Stypocaulon scoparia*, *Gibbula magus* (Linnaeus, 1758) in *Padina pavonica* and *Stypocaulon scoparia*, and the small bivalve *Lasaea adansonii* (Gmelin, 1791) in *Sargassum vulgare* and *Gelidium spinulosum*). COSTA AND ÁVILA (2001) found *Bittium* sp. with high-density values in monospecific samples of *Stypocaulon scoparia* and of *Halopteris filicina*; with lower densities, *Setia subvaricosa*, *Tricolia*

pullus azorica and *Rissoa guernei* were also common molluscs.

The differences detected in the relative abundances of the malacological communities associated to algae, are usually related to different habitat conditions, both biotic (species and type of most common algae, algal biomass, predation intensity) as abiotic conditions (especially the hydrodynamics and the total amount of sediment that algal fronds may trap and hold) (AZEVEDO, 1991a).

Feeding habits may influence mollusc's distribution by depth. *Bittium* sp. and *Tricolia pullus azorica*, the two most abundant taxa, were found along the entire transect. Such distribution may be attributed to their detritivorous

Tabla VI. Resultados de SIMPER. Datos transformados con $\sqrt{\sqrt{x}}$. *Aan*: *Alvania angioyi*; *Aca*: *Alvania cancellata*; *Asl*: *Alvania sleursi*; *Ana*: *Anachis avaroides*; *Bit*: *Bittium sp.*; *Car*: *Cardita calyculata*; *Cra*: *Crassadoma pusio*; *Gib*: *Gibbula delgadensis*; *Juj*: *Jujubinus pseudogravinae*; *Man*: *Manzonia unifasciata*; *Mar*: *Marshallora adversa*; *Nas*: *Nassarius incrassatus*; *Oci*: *Ocinebrina aciculata*; *Par*: *Parvicardium vroomi*; *Ris*: *Rissoa guernei*; *Tri*: *Trichomusculus semigranatus*; *Tpa*: *Tricolia pullus azorica*. Resto de símbolos como en la Tabla IV.

Taxa/Species (%) (Ratio of each taxa/species)	Cumulative %
13.59 – 9.57 – 7.21 – 6.91 – 6.52 – 6.49 – 5.68 – 5.51 (10.00 – 6.49 – 3.77 – 7.71 – 8.01 – 8.86 – 10.24 – 7.97)	61.85
15.50 – 10.11 – 7.33 – 6.95 – 6.88 – 6.45 – 6.42 (9.22 – 6.31 – 8.48 – 6.42 – 7.31 – 7.70 – 5.25)	59.64
19.69 – 13.75 – 9.58 – 9.49 – 6.75 (4.94 – 4.13 – 4.51 – 3.30 – 5.08)	59.26
33.11 – 17.53 (2.79 – 2.58)	50.64
31.72 (2.30)	31.72
32.87 – 15.84 – 15.46 (2.05 – 1.92 – 1.66)	64.17
24.32 – 13.82 – 7.50 – 5.34 (3.18 – 3.32 – 1.72 – 1.59)	50.98
22.71 – 11.35 – 7.82 – 6.33 (3.16 – 1.72 – 1.73 – 1.42)	48.11
28.64 – 15.45 – 8.91 (2.70 – 2.90 – 1.54)	53.00
16.44 – 11.12 – 7.69 – 7.45 – 6.96 – 5.20 – 4.88 – 4.54 – 4.04 – 3.51 – 3.22 (7.74 – 5.97 – 2.81 – 5.98 – 4.26 – 1.66 – 1.69 – 1.54 – 2.03 – 1.59 – 1.67)	75.04
33.88 – 15.39 (2.36 – 1.68)	49.27

habits, although *Tricolia* is thought to feed also on alga tissues and diatoms (FRETTER AND GRAHAM, 1977; BORJA, 1986; GRAHAM, 1988). Shallow-water rissoids (*Alvania angioyi*, *A. mediolittoralis*, *Manzonia unifasciata* and *Rissoa guernei*) as well as deep-water (*Alvania cancellata* (da Costa, 1778) and *A. sleursi*) also feed preferably on diatoms and epiphyte microalgae, as well as on the food trapped by the sediment that accumulates in the base and in the interstices of the branches of algal fronds (FRETTER AND GRAHAM, 1981; GRAHAM, 1988; ÁVILA, 2000b). *Anachis avaroides* and *Nassarius incrassatus* (Ström, 1768) are carnivorous or scavengers (*N. incrassatus*) feeding on small invertebrates, mol-

luscus included. *Marshallora adversa* (Montagu, 1803) probably feeds on sponges (GRAHAM, 1988) and all bivalves herein are suspension feeders.

The methodology followed in this work was effective in the establishment of the zonation of the most common taxa of molluscs, but did not properly answered to the question of the molluscs/alga biological associations. This is only possible with a broadly systematic study of monospecific algae samples (see BULLOCK ET AL., 1990; COSTA AND ÁVILA, 2001).

The time of sampling is also a non-negligible factor. AZEVEDO (1991a) studied the infralittoral communities of molluscs along a period of one year in

Table VII. SIMPER results. Data transformed by $\sqrt{\sqrt{x}}$. Aan: *Alvania angioyi*; Aca: *Alvania cancellata*; Asl: *Alvania sleursi*; Ana: *Anachis avaroides*; Bit: *Bittium* sp.; Car: *Cardita calyculata*; Cra: *Crassadoma pusio*; Gib: *Gibbula delgadensis*; Juj: *Jujubinus pseudogravinae*; Man: *Manzonia unifasciata*; Mar: *Marshallora adversa*; Nas: *Nassarius incrassatus*; Oci: *Ocinebrina aciculata*; Par: *Parvicardium vroomi*; Ris: *Rissoa guernei*; Tri: *Trichomusculus semigranatus*; Tpa: *Tricolia pullus azorica*. Other symbols as in Table IV.

Groups	Average dissimilarity	Taxa/species
s96 / s97	51.10	Man - Par - Ris - Asl - Cra
m96 / m97	56.41	Bit - Par - Cra - Asl
d96 / d97	60.00	Cra - Asl - Tpa
s96 / m96	29.18	Ris - Ana - Aan - Gib
m96 / d96	37.36	Par - Bit
s96 / d96	41.65	Ris - Man - Par - Aan
s97 - m97	52.82	Cra - Par - Bit - Mar - Man - Tri - Aca
m97 / d97	56.28	Bit - Tpa
s97 / d97	58.67	-
(s96-s97) / (m96-m97)	49.92	-
(s96-s97) / (d96-d97)	55.15	-
(m96-m97) / (d96-d97)	52.66	-
(s96-m96-d96) / (s97-m97-d97)	56.22	Cra - Asl - Man - Bit - Par - Aca

two localities of São Miguel Island (Ribeirinha, located in the north and Caloura, in the south shore). During this time, he found that the molluscs' density was higher in the beginning of the summer, decreasing then and reaching its lower values during the winter times. At Ribeirinha, the most abundant species (>1 mm) were *Bittium* sp. *Tricolia pullus azorica*, *Jujubinus pseudogravinae*, *Nassarius incrassatus*, *Parvicardium vroomi*, *Anachis avaroides* and *Ocinebrina aciculata* (AZEVEDO, 1991b).

In this study, with the sole exception of *N. incrassatus*, all other taxa were also the commonest at São Vicente (Capelas) in 1996 and in 1997. These results point

to a remarkable stability in species composition as well as in mean abundance values of the malacological communities associated to macroalgae in the rocky shores of the Azores archipelago, however, *Tricolia pullus azorica*, *Jujubinus pseudogravinae*, *Manzonia unifasciata* and *Crassadoma pusio* were 2 to 4 times more abundant in July 1996 than in 1997, and *Parvicardium vroomi* was commonest in 1997. Some of the species found only in one of the years are accidental (e.g.: *Melarhaphes neritoides*, *Pisinna glabatra*, *Pedipes pedipes* and *Lasaea adansonii*) which belong to the supralittoral, and others are just rare or encountered by chance, as is the case of the not identi-

Tabla VII. Resultados de SIMPER. Datos transformados con $\sqrt{\sqrt{x}}$. *Aan*: *Alvania angioyi*; *Aca*: *Alvania cancellata*; *Asl*: *Alvania sleursi*; *Ana*: *Anachis avaroides*; *Bit*: *Bittium sp.*; *Car*: *Cardita calyculata*; *Cra*: *Crassadoma pusio*; *Gib*: *Gibbula delgadensis*; *Juj*: *Jujubinus pseudogravinae*; *Man*: *Manzonia unifasciata*; *Mar*: *Marshallora adversa*; *Nas*: *Nassarius incrassatus*; *Oci*: *Ocenebrina aciculata*; *Par*: *Parvicardium vroomi*; *Ris*: *Rissoa guernei*; *Tri*: *Trichomusculus semigranatus*; *Tpa*: *Tricolia pullus azorica*. Resto de símbolos como en la Tabla IV.

Taxa/species (%) Ratio of each taxa/species)	Cumulative %
7.32 – 5.25 – 4.85 – 4.83 – 4.51 (1.76 – 1.70 – 1.74 – 1.50 – 2.06)	26.76
5.63 – 5.05 – 4.94 – 4.64 (1.52 – 1.69 – 1.62 – 1.53)	25.57
6.47 – 6.24 – 4.71 (1.46 – 1.72 – 1.66)	17.41
7.57 – 4.64 – 4.40 – 4.32 (3.06 – 1.40 – 1.43 – 1.55)	20.93
5.68 – 4.16 (1.47 – 1.42)	9.84
6.68 – 6.43 – 6.01 – 4.77 (5.97 – 1.54 – 1.76 – 1.58)	26.96
5.53 – 5.02 – 4.38 – 4.10 – 4.07 – 3.88 – 3.55 (2.26 – 2.06 – 1.50 – 1.73 – 1.68 – 1.81 – 2.28)	30.53
6.06 – 5.73 (1.57 – 1.49)	11.79
no taxa/species with ratio > 1.40	-
no taxa/species with ratio > 1.40	-
no taxa/species with ratio > 1.40	-
no taxa/species with ratio > 1.40	-
5.05 – 4.90 – 4.84 – 4.82 – 4.71 – 3.43 (1.60 – 1.49 – 1.40 – 1.44 – 1.55 – 1.58)	27.75

fied Eulimidae, associated with a host. A more detailed study of the population dynamics of their individual species could help to clarify the situation, mainly by stating the role of recruitment on these disparate abundances.

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